SOME THOUGHTS ON ANGIOSPERM PHYLOGENY AND TAXONOMY

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Since the time of Darwin, taxonomists have been concerned with phylogenetic relationships as well as with the formal taxonomic system. Some definitions of taxonomy have essentially equated it with phylogeny, as a study devoted to determining the evolutionary relationships among organisms. More recently, particularly in England, some botanists have tried to divorce taxonomy from phylogeny, reverting in this respect to pre-Darwinian days. Theirs is a natural reaction to the fact that the marriage of taxonomy to phylogeny has proved to be a rather difficult one.

It has become progressively clearer that a precise correlation of taxonomy with phylogeny is an unattainable goal. The more abundant the phylogenetic and other data, the more obvious the impossibility. Over and over again it turns out, when we have enough evidence, that before we can trace the members of a particular group back to a common ancestor, we are outside the confines of the group. The mammals, for which we have a very good fossil record, provide a case in point. No matter what set of criteria one chooses, there was never *an* original species of mammal, from which all other mammals are descended. The mammals originated as a set of more or less parallel evolutionary lines from reptiles—not just any old reptile, but from a particular group of reptiles during a particular span of geologic time. George Gaylord Simpson has for thirty years been using these facts to point out that the monophyletic criterion must be interpreted loosely if it is to be taxonomically useful. One way to put it is to say that if all the members of a particular taxon are descended from another taxon of lesser rank, the taxonomic criterion of monophylesis has been sufficiently met.

Once we admit the necessity for a loose interpretation of the monophyletic requirement, we are committed to the position that similarities due to evolutionary parallelism, as well as those due strictly to inheritance from a common ancestor, provide some indication of relationship and should be considered in the formulation of a taxonomic system. Insofar as the nature of the supply of mutations is a controlling force in evolution, the greater the genetic similarity between two groups, the greater the likelihood that they will produce similar mutations, have similar evolutionary potentialities, and undergo parallel evolutionary change. On phenotypic and genotypic bases, as well as on the basis of the nature of the supply of mutations, different groups have different evolutionary potentialities, and not all evolutionary channels are open to any one group. Insofar as natural selection is a controlling force in evolution, the greater the phenotypic and genotypic similarity between two groups, the greater their potentiality to undergo parallel evolutionary change. If the similarities resulting from parallelism are numerous and pervasive, then the ancestors were probably very similar to begin

with. Thus, a group defined on characters that turn out to reflect evolutionary parallelism may still meet, in some cases, the loose test of monophylesis that we have prescribed.

In spite of these difficulties with the application of the monophyletic criterion to taxonomy, it is clear (at least to me) that phylogenetic considerations have a proper role to play in the establishment of taxonomic systems. The true function of taxonomy is to produce a system of classification of organisms that best reflects the totality of their similarities and differences. Since we have significant data on only a small fraction of the total number of characters of organisms (especially characters that do not have an obvious morphologic expression), the system needs to be set up in such a way that new data, as they are acquired, will tend to fit in harmoniously, rather than being at cross purposes to it. This will be true only if the system is in broad-scale harmony with evolutionary relationships.

It is possible to perceive natural groups without thinking in terms of evolution, as indeed taxonomists did B.D. (Before Darwin), but such perception is facilitated by an evolutionary frame of reference. The transfer of the Salicaceae and Cucurbitaceae from the subclasses Hamamelidae and Asteridae, respectively, to the subclass Dilleniidae reflects evolutionary thinking rather than simple phenotypic comparison in a theoretical vacuum.

The taxonomic system needs to be so constructed that a logically possible and reasonably monophyletic evolutionary scheme can be devised for it. The more information we have, the fewer will be the possible alternatives in such a procedure. On the information available to him, Engler could include the Salicaceae with his other Amentiferae, and treat the Amentiferae as the most primitive group of dicotyledons. On the information available to us now, modern taxonomists can do neither. Bentham and Hooker could insert the gymnosperms between the monocotyledons and dicotyledons, and treat all three groups at the same rank. No one would propose to do so now.

The development of a taxonomic scheme and a phylogenetic interpretation properly proceed in close association, each influencing the other.

The fossil record has only recently begun to be very useful in major taxonomic and phylogenetic interpretations in the angiosperms. The scanning electron microscope has greatly increased the utility of pollen in this regard, and the palynological data have been one of the factors leading to a reconsideration of the megafossils. A comprehensive reinterpretation of the Potomac early Cretaceous angiosperm fossils is underway but not yet published. I do not want to publicly anticipate the results of Drs. Doyle, Hickey, and Wolfe, but I will say that insofar as I am acquainted with these results, they are compatible with my previous views. Doyle has already published enough about fossil pollen to give strong support to the view, originally put forward primarily on the basis of comparison of modern taxa, that the monosulcate pollen type is primitive among the angiosperms.

For the present, at least, comparative structure of modern forms, from the eyeball to the SEM level, remains the mainstay of major taxonomic interpretation. Chemical and serological data of various sorts are beginning to find their use also. The time and effort required to obtain information of these sorts, how-

ever, insures that morphology, in the broad sense, will continue to reign taxonomically supreme for some years to come.

We should recognize, of course, that morphological characters have a chemical foundation. All characters are eventually chemical, and what we commonly call chemical characters are really just the ones without a known morphological expression. Chemical characters, as so defined, are intrinsically neither more nor less significant taxonomically than morphological ones. It all depends on how well they correlate with other characters.

One of the fundamental taxonomic principles that most of us are comfortable with is that taxonomy proceeds by the recognition of multiple correlations. A corollary of this principle is that individual characters are only as important as they prove to be in marking groups that have been recognized on a larger set of information. It is a natural assumption that once the value of a character in a particular group has been established in this way, it can be applied fairly uniformly across the board in other groups. This assumption is false, and has to be unlearned by each successive generation of taxonomists. There is just enough tendency for consistency in the value of taxonomic characters to mislead the unwary. One of my colleagues in another country has summarized the situation by paraphrasing Orwell: All characters are equal, but some are more equal than others.

We often hear the idea nowadays, that when we can get down to the level of the chemical structure of the gene we will have a better set of characters, which will enable us to find out the *real* relationships among organisms. Then we can downgrade or dispense with the traditional phenotypic characters, which lose validity because they are so many steps removed from the genes that govern them. This idea is a beguiling fallacy. Genes are important, not for their own sake, but for what they do. They are important because of their influence on the phenotype. The fundamental concern of human beings in considering organisms is the nature of the phenotype. In order to understand the phenotypes, we begin by trying to distinguish genetic from environmental influences. In pursuit of understanding genetic influences we are led eventually to the gene. Certainly an understanding of the detailed chemical composition and structure of genes is potentially helpful to the taxonomist, and I welcome efforts in this direction. At the same time, we cannot expect to have a high batting average in predicting phenotypic effects from genic composition. A chemical difference that seems small to us might have a disproportionately large phenotypic effect, and vice versa. We can no more predict the phenotype directly from the genes than we could predict the double helix from a study of nuclear physics.

Finally, a bit of philosophizing about how to recognize phylogenetic relationships. We must first recognize that Bessey was right in emphasizing that plant relationships are up and down phylogenetic lines, rather than crosswise. A useful way of perceiving relationships, then, is to find out what is going on in a group, and then mentally extrapolate backwards from the more primitive known members. Oftentimes some other group will then emerge as likely ancestors. Similarities between advanced members of two groups, on the other hand, are significant only insofar as they indicate similar evolutionary potentialities in the

primitive members. As we have pointed out, such similarities are not to be ignored, but they are only part of the evidence, to be weighed along with all the rest of the evidence. The angiosperms as a whole are so beset with parallelism that the taxonomic and phylogenetic significance of individual similarities is often minimal.

One must also put in the caveat that when one taxon is said to be ancestral to another, it does not necessarily mean that any existing member of the first group is the surviving ancestor of the second. It merely means that if we had the ancestor, we would put it in that group. No existing reptile is ancestral to the mammals, but the mammals originated from reptiles all the same.

Let us take the Asteraceae as an example for the extrapolation principle. The fossil record of the Asteraceae is still too scanty to be very useful. On the basis of comparison of modern members of the family, it is clear that aggregation and reduction of the inflorescence have been pervasive features in the evolution of the family. Furthermore, it appears that the primitive composites must have been woody plants with opposite leaves and a basically cymose inflorescence structure. If we then extrapolate backwards from these opposite-leaved, woody plants to something with a less condensed, basically cymose inflorescence, where do we land? Certainly not in the alternate-leaved, essentially herbaceous order Campanulales, which has often been taken as ancestral to the Asteraceae. Instead, the Rubiales and the more primitive members of the Dipsacales are suggested. Even the specialized pollen presentation mechanism, which has been used to link the Asterales to the Campanulales, occurs also in some members of the Rubiaceae. The features here discussed do not prove that the Asterales are derived from the Rubiales or Dipsacales, but they do provide a lead to be investigated. That investigation leads me to believe that the ancestry of the Asterales lies in or near the Rubiales.